Woody species colonisation in relation to habitat productivity

Smit, R.; Olff, H.

Published in:
Plant ecology

DOI:
10.1023/A:1009750216223

Publication date:
1998

Plant Ecology **139:** 203–209, 1998.

Woody species colonisation in relation to habitat productivity

R. Smit & H. Olff
Department of Environmental Studies, Group of Nature Conservation and Plant Ecology, Wageningen Agricultural University, Bornsesteeg 69, 6708 PD, Wageningen, the Netherlands

Received 5 August 1997; accepted in revised form 20 July 1998

Key words: Dispersal mode, Life forms, Life history traits, Old fields, Perennial sward

Abstract

A study was conducted to analyse the effect of habitat productivity on woody species colonisation. Three soil types were distinguished: a relatively poor sandy soil type (1), a somewhat richer sandy type (2) and a relatively rich sandy loamy type (3). Chronosequences were established on these three soil types of 38 (type 1), 20 (type 2) and 54 years (type 3) after abandonment. In total 117 vegetation relevées were used to analyse life form change and species responses during old field succession via regression models. On the rich soil type the colonisation rate of woody species was slower than on the poor soil type. This can be explained by higher abundances of perennial species during the first 20 years after abandonment on the rich soil type in contrast to the poor soil type. Perennial species may delay the woody species colonisation. First they close the bare ground which inhibits germination and next they compete with woody seedlings for light, water and nutrients. The effect of habitat productivity on woody species colonisation can only be determined appropriately by taking life history traits into account. Early successional 'pioneer' woody species dispersed by wind have less difficulties colonising old fields than late successional 'forest' species; they colonise old fields prior to the development of a dense perennial sward. Forest species depend on animals to be dispersed which are attracted by vegetation structure. In $\pm$ 30 years on the poor soil type and in $\pm$ 45 years on the rich soil type woody species become dominant relative to other life forms. Forest species like *Quercus robur* L. invaded relatively early ($<$5 years) in contrast to other studies which probably coincides with the distance to seed sources (forest edges).

Introduction

The filtering effect of initial site conditions on seed dispersal and arrival, seedling establishment and subsequent growth and survival of plant species has a major impact on the secondary vegetation succession (Finegan 1996; Miles 1979). Site conditions like habitat productivity (soil richness) affect the colonisation rate of new species indirectly via competition with initial species for light and nutrients (Finegan 1984; Inouye & Tilman 1995). Mainly grass and forb species are experimentally used to test the inhibition hypothesis based on habitat productivity (Reader et al. 1994). Tilman (1993) suggests mechanisms of how the species richness dependents on habitat productivity; in more productive habitats have more litter accumulation and a lower light penetration inhibiting the establishment of new species. Besides grasses and forbs, woody species play an important role during the secondary succession. The vegetation succession on old fields generally proceeds towards forest (Pickett 1982; Monk 1983). Since most temperate woody species do not form seed banks (Burrows 1990; Milberg 1995), they have to colonise old fields by seed rains from 'outside'. Therefore, arable weeds which do form a seed bank are the first to colonise. Thus, before woody species can attain dominance, they have to compete with the initial, herbaceous vegetation. Desteven (1991b) proved the competition between woody species and the initial vegetation to be a major determinant of woody species growth and survival. The colonisation of woody species can only be analysed appropriately when life history traits are considered. As suggested by Finegan (1984) early

successional, 'pioneer' woody species have as compared to late successional woody species ('forest species') different plant attributes such as dispersibility and juvenile growth. Pioneer species are merely wind-dispersed and have fast juvenile growth rates as compared to forest species which are mainly animal-dispersed and have slow juvenile growth rates. In general pioneer species have faster colonisation rates than forest species. Several theories have been developed to describe forest succession in which habitat productivity is taken into account (Egler 1954; Connel & Slatyer 1977). Occasionally long term old field studies are reported (Pickett 1982; Osbornova et al. 1990) but no comparison of how woody species invasion depends on habitat productivity gradient has yet been made. We studied when woody species colonise old fields (1) and how fast they establish as dominant species as influenced by habitat productivity and life history traits (2).

Methods and materials

Study areas and plots

Old field succession was reconstructed using chronosequences. In total 117 old field relevées were used consisting of 80 different old field locations with a known year of abandonment. In large old field complexes more than one relevée was recorded. The relevées were taken in old fields on sandy soils, distributed in the eastern part of the Netherlands. This Pleistocene part of the Netherlands is dominated by dry, poor, coversand soils and is influenced by a sea climate, based on a mean annual rainfall of 650–700 mm and a mean annual temperature of 9.5-10.0 °C (Ormeling 1971). Most of these fields were former corn fields (*Zea mays* L..

The relevées were recorded using 10 × 10 m sample plots. This large size of the sample plot obtained a reliable reflection of the old field vegetation, which is frequently heterogeneous. The abundance (% cover) of each species was estimated visually, using subplots (5×5 m) to estimate more accurately. The sample plots were placed in homogeneous vegetation parts and in the centre of the old field; to be representative for the species occurrence and composition of the particular old field vegetation, and to prevent side effects.

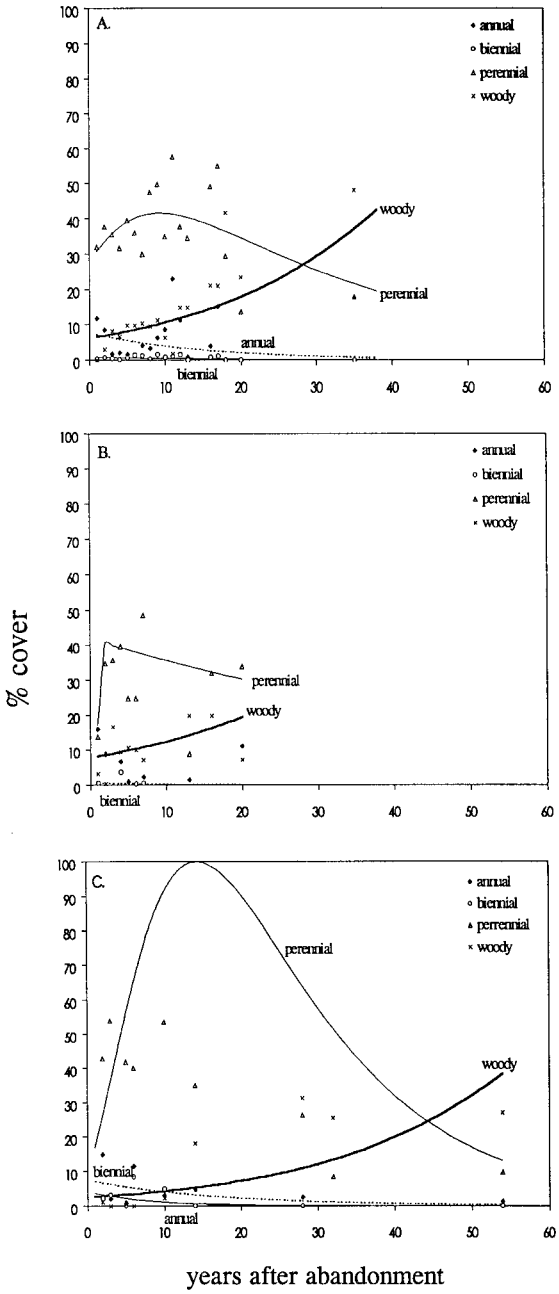

Figure 1. The fitted changes in life forms and observed values during old field succession on (A) Soil type 1: poor; podzolic sandy, (B) Soil type 2: richer: podzolic, sandy earthy, (C) Soil type 3: rich, earthy sandy, using the models of Huisman et al. (1993).

Data analysis

Old field succession was reconstructed using chronosequences of three soil types. The classification was based on various discriminating parameters like par-

Table 1. The characteristics of the soil types (de Bakker & Schelling 1976). Age= maximum age of old field, Number= number of relevées, HGL= mean highest ground water level, Organic layer= depth of organic layer, pH=pH of ground water.

Soil type	Age	Number	Parent material	HGL	Organic layer	pH
1	38	88	sand	> 80 cm	< 15 cm	± 5
2	20	17	sand	> 80 cm	15–30 cm	± 5
3	54	12	sand-loam	< 40 cm	> 30 cm	5–6

ent material, depth of organic layer, pH and depth of ground water, using the Dutch soil classification according to Bakker & de Schelling (1976). The soil parameters were sampled in the field using a soil drill and a portable, WTW microprocessor pH meter.

The 117 relevées were subdivided into a poor, podzolic, sandy type (1), a somewhat richer, podzolic, sandy, earthy type (2) and a relatively rich earthy type (3) (Table 1). The chronosequences of the soil types were limited to 38 (type 1), 20 (type 2) and 54 (type 3) years after abandonment. The colonisation of woody species was analysed in two ways: (i) analysis of life form change during old field succession per soil type, and (ii) a species response analysis of the main woody species in comparison to dominant forbs and grasses.

The trends in life form change during old field succession were established using the statistical models of Huisman et al. (1993). The dominant species were used to characterise the species responses during the chronosequences. Besides the woody species that occur in >25% of the relevées per soil type, the forbs and grasses with a mean abundance >5% over the whole period of the sequence and occur in >25% of the relevées (per soil type) were selected. Some species of the same genus were added because they showed a similar pattern of occurrence and acted as dominant, perennial competitors with woody species (Table 2). The woody species were subdivided into pioneer and forest species based on the empirically determined plant attributes according to Finegan (1984) (Table 2).

Per age the abundance of the life form or species was mediated and arcsine ($\sqrt{y/100}$) transformed prior to the analysis, which reduced the heterogeneity of the error variance. Also the regression models of Huisman et al. (1993) were used to determine the species responses during old field succession.

Table 2. The life forms and species used for the regression analysis. P= pioneer, F= forest species. Life forms: P= perennial, W= woody, A= annual, B= biennial. *Betula spp*= *Betula pendula* Roth+*Betula pubescens* Ehrh., *Salix spp*= *Salix caprea* L.+*Salix aurita* L., *Holcus spp*= *Holcus mollis* L.+*Holcus lanatus* L., *Agrostis spp*=*Agrostis tenuis* Sibth.+*Agrostis stolonifera* L.

Species	Succession (P, F)	Life form (P, W, A, B)
Quercus robur L.	F	W
Betula spp	P	W
Alnus glutinosa (L.) Vill.	P	W
Salix spp	P	W
Prunus serotina Ehrh.	F	W
Holcus spp	–	P
Agrostis spp	–	P
Urtica dioica L.	–	P

Results

Changes in life forms

The life form changes during old field succession were more or less similar on the three soil types (Figure 1). During the first 20 years after abandonment:

- A relatively high abundance of annual and biennial species during the first 5 years followed by a decrease.
- An increase of perennial species up to a peak abundance (40–100% cover) at 10 years after abandonment followed by a decrease.
- An increase of woody species abundance.

The difference in abundance of perennial species between the soil types is remarkable; a high abundance on soil type 3 relative to soil type 1 and 2 during the first 5 years. The woody species started to dominate the vegetation after ± 30 years on soil type 1 and after

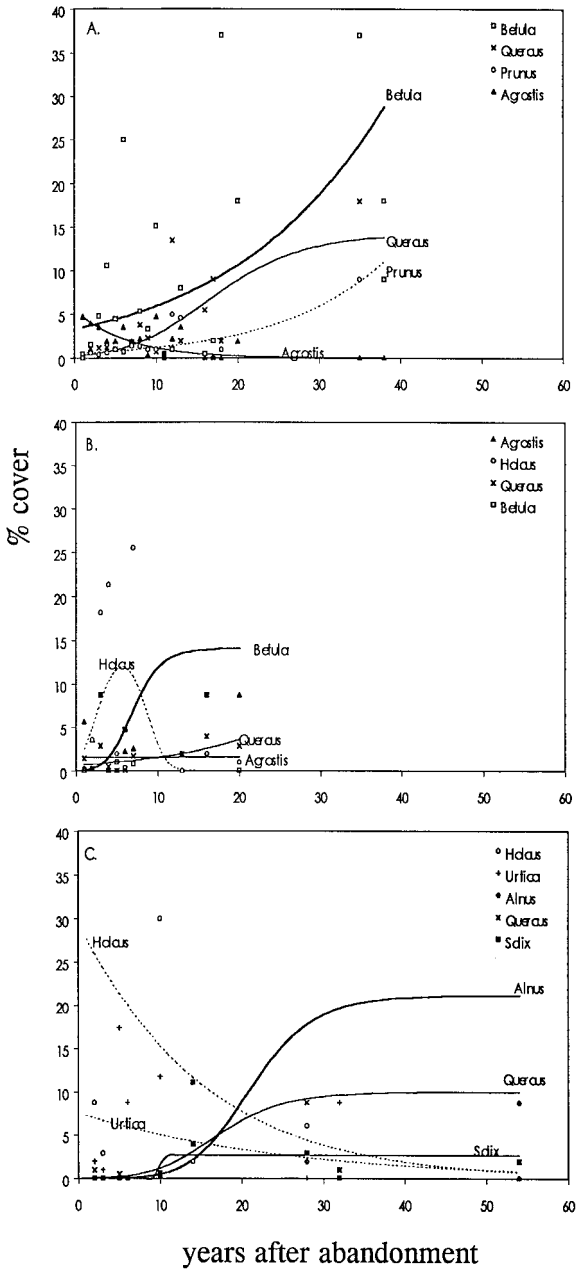

Figure 2. The fitted changes in species abundance and observed values during old field succession on soil types 1 (A), 2 (B) & 3 (C) according to the models of Huisman et al. (1993).

± 45 years on soil type 3. The vegetation succession on soil type 2 is still dominated by perennial species after 20 years of abandonment. The colonisation of the woody species on the soil types appeared to differ strongly (Figure 1). On soil type 3, the woody species colonisation started at a lower level of abundance and proceeded slower as compared to soil type 1.

Trends of individual species

On soil type 1, the vegetation was dominated by *Agrostis spp* during the first 5 years. Than after ± 10 years *Betula spp* starts to become dominant; its abundance rapidly increased from 5% to 30% cover in ± 20 years, while the abundance of *Agrostis* spp declined strongly. The 'forest' species *Quercus robur* and *Prunus serotina* slowly increased until an abundance >10% after 35 years of abandonment. The trend of *Prunus serotina* is still increasing while *Quercus robur* tend to have reached a constant level.

On soil type 2 the abundance of the perennial species *Holcus* spp had a peak occurrence after 5 years of abandonment at ±10% cover and then strongly declined to zero% cover, while *Agrostis* spp. had a constant level of 2–3% during the first 20 years after abandonment. *Betula* spp strongly increased from 1–3% to ±15% cover. The forest species *Quercus robur* played a minor role during this period; the abundance increased slowly from 1–4%.

On soil type 3 the vegetation was initially dominated by perennial species (Figure 1c) like *Holcus* spp and *Urtica dioica* (Figure 2c). The abundance of *Holcus* spp and *Urtica dioica* strongly declined in 30 years from respectively 27% and 7% to <5% cover. Pioneer woody species like *Alnus glutinosa* and *Salix* spp were present in the first 20 years where *Salix* spp. played a minor role at a level of ±4% reached after 10 years and remaining constant during the further years. *Alnus glutinosa* started to be dominant after respectively 20 years of abandonment and reaching a level of ±20% cover after 30 years of abandonment. The occurrence of *Quercus robur* slowly increased to a constant level of ±10% cover in 30 years of abandonment.

In general, the initial woody species were all pioneers while forest woody species followed the pioneers until an abundance of 10–15% after 38 years on soil type 1, 3% after 20 years on soil type 2 and 10% after 54 years on soil type 3.

Discussion

When analysing the change of life forms during old field succession on the three soil types, a relatively fast establishment of woody species was found (>5%

Table 3. The models of Huisman et al.[1] (1993) fitted on data of life forms during old field succession on soil type I, II and III. Per life form the proportion variance 'explained' (R^2), the degrees of freedom (D.f.) and the model parameters (*a*, *b*, *c*, *d*) are reported.

Life form	Soil type	Model	R^2	D.f.	*a*	*b*	*c*	*d*
Woody	I	II	0.52	17	5.87	−2.73		
Perennial	I	V	0.14	17	−0.45	−0.2	4.58	0.018
Biennial	I	II	0.21	17	6.88	3.34		
Annual	I	II	0.19	17	5.77	3.43		
Woody	II	II	0.18	8	5.86	−2.37		
Perennial	II	V	0.26	6	4.95	0.96	23.3	−2375.15
Biennial	II	II	0.11	8	7.18	8.76		
Annual	II		0[2]					
Woody	III	II	0.54	7	6.32	−2.64		
Perennial	III	IV	0.81	7	4.07	2.93	−0.13	
Biennial	III	II	0.37	7	6.08	6.72		
Annual	III	II	0.32	7	5.78	3.14		

[1](I): $y = M/(1+e^{a})$, (II): $y = M/(1+e^{a+bx})$, (III): $y = M/(1+e^{a+bx})$* $1/(1+e^{c})$, (IV): $y = M/(1+e^{a+bx})$* $1/(1+e^{c-bx})$, (V): $y = M/(1+e^{a+bx})$* $1/(1+e^{c+dx})$, where y =% cover, M =upper bound, x =years after abandonment and *a*, *b*, *c* & *d* are parameters. [2]A too bad fit to report R^2 values (R^2<0.1).

cover in 5 years). This pattern differs from other old field studies woody species remained in lower abundances during the first 10 years was ascertained (Bard 1952; Bazzaz 1975; Pickett 1982; Monk 1983). In this study, probably the proximity of seed sources has affected the colonisation rate of woody species positively. Most of the old fields were located nearby (<100 m) seed sources (forest edges).

The general pattern of life form change showed a similar pattern as compared to above-mentioned studies. Concerning the different roles of the perennial species on the soil types, a habitat productivity effect could be seen. A relatively long dominance of perennials on the rich soil type 3 in comparison to a relatively short-time dominance of perennials on the poor soil type 1. In that case, the abundance of perennials which is directly affected by habitat productivity, may cause higher competition intensity with woody species on rich soils as compared to poor soils. This results in a lower colonisation rate of woody species on rich soils in contrast to poor soils. The chronosequence of soil type 2 was limited to 20 years after abandonment where it is probably in an early stage of vegetation succession as compared to soil type 1 and 3.

According to Gill & Marks (1991) the competition with herbs, especially aboveground competition, reduced growth of woody seedlings. The strong competition for light, water and nutrients with dominant perennial species may severely hinder the establishment of woody species. However, dispersal or germination may be even more critical. If woody species have reached old fields via dispersal vectors like wind or animals their germination and thus final establishment depends on the abundance of the initial vegetation dominated by perennials. Seeds of woody species need bare, mineral ground to germinate; wind-dispersed species in particular. The 'perennial window' presumably closes faster on productive soils as compared to less productive soils that prevent further establishment by woody species (Figure 1a,c). This may declare the even-aged, uniform stands of wind-dispersed pioneers like *Pinus* spp or *Acer* spp on old fields (Rankin & Pickett 1989). These species colonise old fields prior to the development of a dense sward of perennial species. On less productive soils pioneer woody species probably outcompete perennials earlier than on productive soils where especially the competition for light will take longer. In Figures 2a and 2c the shading of woody species may cause the decrease of the abundance of perennial species. Competition for light is the most likely explanation for this pattern.

Until now only the role of pioneer woody species have been discussed. The mature forest species like *Quercus robur* appeared to play a minor role during these stages of old field succession. The role of *Quercus robur* is remarkable; it seems to be present within the early period of secondary succession. Finegan (1984) and McDonnel & Stiles (1983) report an increasing dominance of forest species during old field succession as affected by vegetation structure. In a

Table 4. The best logistic models[1] ($p < 0.05$) (Huisman et al. 1993) fitted on continuous data of dominant species during old field succession on soil type I, II and III. Per species the proportion of variance 'explained' (R^2), the degrees of freedom and the model-parameters (*a*,*b*,*c*) are reported.

Species	Soil type I	model	R^2	d.f.	*a*	*b*	*c*
Betula spp.	I	II	0.30	17	6.19	−0.03	
Quercus robur	I	III	0.61	16	1.88	−0.16	5.44
Prunus serotina	I	II	0.41	17	7.10	−0.04	
Agrostis spp.	I	II	0.52	17	5.94	0.08	
Betula spp.	II	IV	0.78	7	−6.14	0.71	10.50
Quercus robur	II	II	0.32	8	7.01	−0.04	
Agrostis spp.	II	II	0.18	8	6.59	−0.04	
Holcus spp.	II	IV	0.26	7	6.51	−0.68	−1.10
Alnus glutinosa	III	III	0.53	6	3.92	−0.22	5.23
Quercus robur	III	III	0.81	4	2.78	−0.21	5.63
Salix spp.	III	III	0.49	6	−6.75	6.31	
Holcus spp.	III	II	0.35	7	5.05	0.04	
Urtica dioica	III	II	0.21	7	5.77	0.02	

[1] See Table 3.

structural diverse vegetation potential seed dispersers like jays (*Garrulus glandarius* L.) and wood mice (*Apodemus sylvaticus* L.) will be attracted and consequently disperse the seeds of forest species into the old fields. Probably the relatively early arrival of *Quercus robur* in this study has been affected by the distance to the seed sources and not by vegetation structure. Probably, when seed sources are close to the old field, relatively heavy seeds of forest species like *Quercus robur* are dispersed by barochory rather than zoochory. Considering *Prunus serotina*, a similar mechanism is at work. Many old fields are colonised by *Prunus serotina* from nearby forest edges because of the foraging behaviour of frugivorous birds like *Turdus* spp (Snow & Snow 1988). In general it clearly emphasises the importance of life history traits (dispersal mode) during old field succession; if nearby seed sources of forest species are not available the invasion of these species may take long (Wilson 1993).

Analysing the application of succession theories considering the woody species colonisation; the tolerance model (Egler 1954) based on the early occurrence of both pioneer and late forest species is only applicable when seed sources of woody species are nearby. Otherwise the establishment of woody species is inhibited by the actual perennial species which is affected by habitat productivity (Connel & Slatyer 1977; Pickett et al. 1987). In fact, then especially forest species depend largely on the facilitation of vegetation structure via zoochorous dispersal.

Acknowledgements

We are grateful to the people who helped us during the study. Especially W. P. Daamen and E. C. J. Ott for providing the data used in this study. We thank A. K. M. Masselink, A. Oosterbaan, J. den Ouden, and J. Bokdam for help during the preparation of the manuscript.

References

Bakker, H. de & Schelling, J. 1976. Systeem van bodemclassificatie voor Nederland, de hogere niveaus. Pudoc, Wageningen.

Bard, G. 1952. Secundairy succession on the Piedmont of New Jersey. Ecological Monog. 22: 195–216.

Bazzaz, F. A. 1975. Plant species diversity in oldfield successional ecosystems in southern IlIinois. Ecology 56: 485–488.

Burrows, C. J. 1990. Process of vegetation change. Unwin Hyman, Boston, Sydney, Wellington.

Connel, J. H. & Slatyer, R. O. 1977. Mechanisms of successions in natural communities and their role in community tability and organization. Am. Nat. 111: 1119–1144.

Debusche, M., Escarre, J. & Lepart, L. 1982. Ornithochory and plant succession in mediterranean orchards. Vegetatio 48: 255–266.

DeSteven, D. 1991a. Experiments on mechanisms of tree establishment in old-field succession: seedling emergence. Ecology 72(3): 1066–1075.

DeSteven, D. 1991b. Experiments on mechanisms of tree establishment in old-field succession: seedling survival and growth. Ecology 72(3): 1076–1088.

Egler, F. E. 1954. Vegetation science concepts. Initial floristic composition, a factor in old-field vegetation development. Vegetatio 4: 412–417.

Finegan, B. 1984. Forest succession. Nature 312: 109–114.

Finegan, B. 1996. Pattern and proces in neotropical secondary rain forests: the first 100 years of succession. TREE 11: 119–123.

Gill, D. S. & Marks, P. L. 1991. Tree and shrub seedling colonization of old fields in central New York. Ecological Monographs 61(2): 183–205.

Huisman, J., Olff, H. & Fresco, L. F. M. 1993. A hierarchical set of models for species response analysis. J. Veg. Sci. 4: 37–46.

Inouye, R. S. & Tilman, D. 1995. Convergence and divergence of old-field vegetation after 11yr of nitrogen addition. Ecology 76(6): 1872–1887.

McDonnel, M. J. & Stiles, E. W. 1983. The structural complexity of oldfield vegetation and the recruitment of bird-dispersed plant species. Oecologia (Berlin) 56: 109–116.

Miles, J. 1979. Vegetation dynamics. Chapman and Hall, London.

Milberg, P. 1995. Soil seed bank after 18 years of succession from grassland to forest. Oikos 72(1): 3–13.

Monk, C. D. 1983. Relationship of life forms and diversity in oldfield succession. Bull Torrey Bot Club 110: 449–453.

Ormeling, F. J. 1971. De grote bosatlas. Wolters-Noordhoff, Groningen.

Osbornova, J., Kovarova, M, Leps, J. & Prach, K. 1990. Succession in abandoned fields. Kluwer Academic Publishers, Dordrecht.

Pickett, S. T. A. 1982. Population patterns through twenty years of oldfield succession. Vegetatio 49: 45–59.

Pickett, S. T. A., Collins, S. L. & Armesto, J. J. 1987. Models, Mechanisms and Pathways of Succession. Bot. Rev. 53: 335–371.

Rankin, W. T. & Pickett, S. T. A. 1989. Time of establishment of red maple (*Acer rubrum*) in early oldfield succession. Bull. Torrey Bot. Club 116(2): 182–186.

Snow, B. & Snow, D. 1988. Birds and berries: a study of an ecological interaction. Calton, Poyser.

Tilman, D. 1993. Species richness of experimental productivity gradients: How important is colonization limitation? Ecology 74(8): 2179–2191.

Wilson, M. F. (1993) Dispersal mode, seed shadows, and colonization patterns. Vegetatio 107/108: 261–280.